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A Study of the Activities of a Pair of *Galago senegalensis moboli* in Captivity, Including the Birth and Postnatal Development of Twins.

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(Plates I-VI).

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INTRODUCTION.

Galagos, small, elusive lemuroids of arboreal and nocturnal habits, are found exclusively in Africa, where they are well known and widely distributed. Though the anatomical features of the many varieties of these animals have been studied, little seems to have been reported concerning the ways in which their structures function, nor is there any sufficient record of galago habits and family life. The account is spotty and incomplete, partially at least, because their nocturnal and tree-dwelling habits render observation difficult in the field and in captivity. In a study of the galago in captivity, an effort must be made to reproduce in some measure certain elements of its native environment, such as perching structures, space for jumping and dark places for retirement during daylight hours. The nocturnal habits of the group necessitate the observer's continuous occupancy of the animals' night quarters.

For more than three years, beginning September, 1937, I have made a close study of a pair of *Galago senegalensis moholi* A. Smith, a subspecies

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of galago found in abundance throughout the savanna country of central and southern Africa. The opportunity to study these unique and interesting forms was enlarged by the fortunate birth of twins in captivity, making a family of four. Thus it has been possible to add, to the story of the behavior and disposition of the adults, a record of the birth and development of a male and female in captivity. While in the following discussion I have emphasized observations of their habits and family life, I have also described the functioning of those structures which are characteristic of the galago.

DESCRIPTION OF Galago senegalensis moholi.

The Galago s. moholi is a small, round-headed animal with a shortened face; large, almost naked, membraneous ears with transverse ridges; round, wide-open eyes with vertical pupils, and a short rhinarium situated high on the face (Pl. I, Fig. 1).

The body length including the head of the adult male is $6\frac{1}{2}$ inches and the long, non-prehensile tail, which is used for balancing, $8\frac{1}{2}$ inches. The front limbs are shorter than the long hind limbs. The foot, which is highly specialized for jumping, has elongated calcaneum and navicular bones, providing adequate leverage for spectacular jumps.

The opposable huge hallux and less well developed pollex are primate characteristics possessed by the galago, as are the small, and in this species flattened, nails found on all the digits with the exception of the index toe. Here a claw, characteristic of the Lemuroidea, is found.

The dental formula of the Galago s. moholi, like that of the true lemurs, is

 $\frac{2 i}{2}$ $\frac{1 c}{1}$ $\frac{3 p}{3}$ $\frac{3 m}{3}$ = 36 total

The two pairs of procumbent lower incisors are flanked by modified canines, making the typical lemuroidean "tooth-comb."

The neck of the galago is short. The pelage is soft, heavy and almost chinchilla-like. The color of this subspecies is a mottled slate gray and silver with a light brown wash on the dorsal surface of the posterior half of the body. The ventral surface is largely white with slate gray on the deeper portions of the fur, seen only when the fur is separated.

On the inner surface of both arms and legs and across the chest, the pelage is clear yellow. There are white markings on the nose, around the neck and lower jaw. Through the usual gray of the dorsal pelage, longer black hairs protrude sparsely (Pl. IV, Fig. 9). There are black markings around the eye and along either side of the nose from the eye toward the upper lip (Pl. I, Fig. 1). The pelage is shorter near the hands and feet, and more silvery in color.

There are no well defined sex differentiations. The adult male is slightly larger than the female and the yellow of the pelage perhaps more marked. The length of the tails in this group varies between $8\frac{1}{2}$ and 10 inches. (The tail of the adult female under discussion is unnaturally short because of an injury to the tip sustained at capture (Pl. V, Fig. 12).

HISTORY AND CLASSIFICATION-PALEONTOLOGY.

In 1796 Étienne Geoffroy-St. Hilaire first described one of the "quadrumana" which the natives called "Galago," found in western Africa in the region of Senegal. A skull of this form was brought to him at the Museum in Paris by Michael Adanson who had spent some years in exploration of 1940

the Senegal, and a skin was later provided by the Duc de Nivernais. The addition of pictures and descriptions furnished by Adanson led Geoffroy to the conclusion that this was a new type of animal which resembled in many respects the makis (lemurs), the lorises, and tarsier. It differed from each of these, however, to such an extent that he felt justified in calling this a new species intermediate, perhaps, between the *Loris* and the *Tarsius*. He determined to adopt for it the native name "Galago" to which he attached "du senegal," perhaps to distinguish it from two other forms (one larger and one smaller) which Adanson had reported to be present in that region. He described¹ it as possessing hind legs longer than the body, built for jumping; the front legs short; the tail longer than the body; ears large and membranous with transverse ridges.

Like the lemurs there were nails on hands and feet with the exception of the second toe which had a claw. The hind foot was very long due to the elongation of the calcaneum and scaphoid (navicular). The fur was grayishtan on the dorsal surface and white with yellow on the under surface. It was also shorter on the hands and head while the under side of the hands and feet and the ears and nose were naked. The animal was described as arboreal and insectivorous. Geoffroy incorrectly stated that there were but one pair of upper incisors.

In 1836 Sir Andrew Smith described a galago of similar size which he found near the Limpopo River, Bechuanaland, South Africa, which closely resembled Geoffroy's *senegalensis*, but differed from it in two features.

- 1. On the ventral surface of the body the fur was white on the tips of the hair only; near the body it was slate gray.
- 2. There were two pair of incisors on the upper jaw instead of one pair as described for *senegalensis*.

On the basis of these differences he felt compelled to consider this a new species and called it *Galago moholi*, which is the Bechuana name for the animal in that locality.

"Had the upper jaw on this species not been furnished with four cutting teeth I should have been disposed to have considered it as identical with *Galago* senegalensis of Geoffroy." (Page 42).

For some years thereafter, the few species of galagos known were classified in accordance with the number of upper incisor teeth described for each. When, however, in 1851 Isadore Geoffroy-St. Hilaire reported that all galagos normally possessed two pair of upper incisors, the main reason for separating *Galago senegalensis* from *Galago moholi* disappeared.

"Les Galagoides de M. Smith sont les espèces qui n'auraient que deux incisives supérieures, et par conséquent trente-quatre dents en tout. Tels seraient, suivant lui les *Galago senégalensis* et *demidoffii*. Cette charactéristique est erronée; ces espèces ont normalement quatre incisives supérieures comme les autres; seulement deux sont caduques, comme il arrive si souvent chex les Lémurides." (Page 80.)

The Galago moholi is now recognized as a sub-species of Galago senegalensis. According to W. L. Sclater, 1900, (Page 23),

"This little Lemur is closely allied to the West African form with which it has frequently been confounded, but an examination of the two species (*Galago* senegalensis in Paris and *Galago* moholi in London) shows that they are really distinct."

According to E. Schwarz (1931), the Galaginae fall naturally into two genera: (1) *Euoticus* with pointed nails; (2) *Galago* with flat nails. *Euoticus* is represented by a single species (*elegantulus*). Members of the genus

¹ The dimensions were given as follows:

Body length 6 inches	10 lines
Tail length 8 inches	4 lines
Head length 1 inch es	8 lines
Anterior limbs 3 inches	
Posterior limbs including feet 6 inches	11 lines

Galago, however, are numerous and Schwarz divides them provisionally into four species:

- 1. Galago crassicaudatus
- 2. Galago alleni
- 3. Galago demidoffii
- 4. Galago senegalensis²

The Galaginae, because of their long tails and ability to jump, are called "African long tailed Lemurs;" other anatomical details, however, relate them more closely to the short tailed, climbing, loris-like forms of Asia and Africa. The current classification of the Lemuroidea provides for two main divi-sions, the Lemuriformes and the Lorisiformes (W. K. Gregory, 1916), subdivided as follows:

Suborder Lemuroidea³

Division A. Lemuriformes—all inhabitants of Madagascar

Family 1. Lemuridae Family 2. Indrisidae

Family 3. Chiromydae

Division B. Lorisiformes-Inhabitants of Asia and Africa

Family 1. Lorisidae⁴

[•] Subfamily 1. Lorisinae

Arctocebus-West Africa

Perodicticus-West Africa

Nucticebus-N. India to Philippine Is.

Loris-S. India, Ceylon

Subfamily 2. Galaginae

Euoticus—Tropical and subtropical Africa *Galago*—Tropical and subtropical Africa

Palaeontologically the time and place of origin of the Lorisiformes, unlike those of the Lemuriformes and the Tarsioids, are obscure because of total lack of fossil evidence. Dr. George Pinkley of the American Museum of

² R. W. Hayman (1937) further emphasized the difference in nail structure among the Galaginae. He demonstrated that crassicaudatus has concave nail ends while demidoff if Fischer, alleni Water-house and senegalensis Geoffroy all have nails which are bluntly rounded at the ends with the exception of Galago senegalensis invasues Schwarz. Because this form possesses pointed and keeled nails he is convinced that invasues Schwarz should have the status of a new species.

³ The relation of the Lemuroidea to other primates is not the function of this article; however, a brief outline of recent trends in Primate classification may be pertinent.

Classification of

Pocock—Zuckerman (1918) (1933) Order Primates

rder Primates Series 1. Strepsirhini Suborder Lemuroidea Div. A. Lemuriformes Div. B. Lorisiformes Series 2. Haplorhini Suborder Tarsioidea Suborder Tarsioidea

Allen-Coolidge modification of Pocock. Allen-Coolidge modification of Pocock, Schwarz. Zuckerman, as outlined by R. M. and A. W. Yerkes, 1935 Order Primates Division 1. Prosimiae Suborder 1. Lemuroidea Suborder 2. Tarsioidea Division 2. Anthropoidea

Dr. George G. Simpson is now (1940) revising his classification, the main outline of which, exclusive of fossil forms, is as follows:

Order Primates Suborder Prosimii

aborder Prosimi Infraorder Lemuriformes Superfamily Tupaioidea (Tree or squirrel shrews) Superfamily Lemuroidea (Malagasy lemurs and lemuroids) Infraorder Lorisiformes (Lorises, pottos, galagos—no fossil forms) Infraorder Tarsiiformes (Tarsius and fossil tarsioids)

Suborder Anthropoidea

While the relation of the Lemuriformes and the Lorisiformes is not changed, the term Lemuroidea is relegated to that of a superfamily instead of the more inclusive one of suborder, and the term Lemuriformes includes the primitive Tupaiodea as well. The Tarsioids, as in the case of the Allen-Coolidge modification, are put back once more with the Prosimii.

⁴ Some authors rank the two subfamilies as families, Lorisidae and Galagidae, respectively. In that case no subfamilies are indicated.

Natural History, in the following memorandum to the author (1940) elaborates this statement as follows:

"The occurrence of fossil specimens of the lower primates indicates that in the geologic past the geographic distribution of these forms was singularly different from that of today. Specimens representing the Lemuriformes and Tarsioids (but not the Lorisiformes—lorises, pottos, and galagos), are found in fossiliferous deposits in both Europe and western North America. They are first known from middle Paleocene formations in America, seem to have spread over holarctic regions and appear in late Paleocene deposits of Europe. They range through the Eocene, disappear in the late Eocene in Europe but not until the early Oligocene in America. Lower primates are then quite unknown in the fossil record until the appearance of Lemuroids in the late Pleistocene of Madagascar, where they are now confined. And *Tarsius*, living today in the Malay archipelago, is the only surviving representative of the Tarsioids. This leaves a hiatus in the fossil record of nearly two-thirds of Cenozoic time—about forty million years.

"It is furthermore remarkable that the paleontological history of the Lorisiformes is entirely unknown although living forms are widely distributed through tropical Africa and the Indo-Malayan region. It is true that the French Eocene forms *Pronycticebus* and *Pseudoloris* were formerly believed to represent fossil Lorisoids, but more careful examinations indicate that they represent a Lemuroid and a Tarsioid, respectively. There is good reason, from comparative anatomical studies, to believe that the ancestry of Lorisiformes is approximately as ancient as is that of Lemuriformes. It therefore seems probable that during the time when the fossil record of Lemuriformes and Tarsioids was accumulating in limited areas in Europe and western North America, early Lorisoids were living in some other part of the world—possibly Asia or Africa."*

DISTRIBUTION.

Euoticus, Galago alleni and *G. demidoffii* are forest dwellers, while the six varieties of *crassicaudatus* and ten varieties of *senegalensis* are found only in the savanna country, a type of environment defined by botanists as "grassland with scattered shrubs and medium-sized trees." (J. Chapin, 1933, page 103). According to Shortridge (1934), typical *senegalensis* and other races of the species range through Africa to as far north as Senegal, Nigeria, French Equatorial Africa, the Southern Soudan, Gallaland, and Somaliland and as far south as Inhambane in Portuguese East Africa, but apparently not south of the Southern Transvaal. According to Sclater (1900), Schwarz (1931) and Shortridge (1934), the subspecies *moholi* is widely distributed over eastern, southeastern, southern and southwestern Africa, in the north at least as far as the Tabora district in Tanganyika Territory, possibly extending further northwest.

CONDITIONS OF OBSERVATION.

For the first two winters, I shared the same room with the adult pair of galagos. During the day, the animals were confined in a cage $6 \times 4 \times 4$ feet. On a shelf in the cage was a small sleeping box which provided the needed darkness. At night for periods of two to five hours, they were liberated and given the freedom of the room for exercise. A shaded light made observation possible without distress to the animals. By placing food on their feeding shelf, they were finally coaxed back into the cage. While sharing a room with a pair of galagos had obvious disadvantages to the observer, nevertheless, it offered the surest method of obtaining detailed data throughout their active period. During the exercise period, all damageable articles were covered with sheets. At frequent intervals the walls of the room were washed down.

^{*} According to Dr. W. K. Gregory the removal of *Pronycticebus* from the Lorisidae to the Adapidae by Dr. G. G. Simpson (1940) deprives the Lorisoids of any known early Tertiary representative.

From June to September, the galagos were removed to the country, where they enjoyed the complete freedom of a screened-in porch 10×14 feet, adjoining my room. As usual, they slept in a sleeping box on a shelf. Several times each night their activities were checked.

The birth of the young galagos occurred in the second spring, April, 1939, in the apartment room, under the most favorable conditions for continuous observation.

The third winter, when the young animals were half-grown, the inconvenience of caring for so large a family made advisable their transfer to a 10×7 feet partitioned section of a heated greenhouse on the roof of Barnard College, Columbia University. While conditions now prevent a constant watch, some record of activity is made at varying intervals, at least three times each night, twice by myself and once by the night watchman.

In the daytime the animals sleep fairly continuously. A darkened and elevated recess in the cage, greenhouse or porch protects them from the sunlight. Their quarters are kept scrupulously clean by frequent scrubbing.

In both the greenhouse and the screened-in porch, small growing trees planted in tubs have been provided, as well as horizontal and vertical round, wooden, exercise bars. One side of the porch is screened by half-inch meshing, large enough to admit moths, the galagos' favorite fare. The moths and other insects are attracted by a light with a reflector situated in the enclosure.

Full-sized doors leading into both the greenhouse enclosure and porch make it convenient for visitors to enter and watch at close range the behavior of the galago family.

The *Galago s. moholi* seems to be hardy. It can tolerate a wide range of temperatures from summer heat of more than 90 degrees in their sleeping box to as low as 40 degrees on a cold winter night.

FUNCTIONING OF THE STRUCTURES CHARACTERISTIC OF THE GALAGO.

It is my purpose at this point to supplement the outline of the known features of the adult *Galago s. moholi* by further details based on my own observations of the functioning of the outstanding structures which differentiate this form. From time to time when possible I have attempted to compare these structures with those reported of closely related lemuroids, as well as with *Tarsius*, which, while not so closely related, displays many interesting similarities and differences.

The Head.

a. Facial Expression. b. Lips. c. Nose.

The galagos, like the Lemurs, are extraordinarily expressionless—"notoriously blank," as S. Zuckerman has expressed it. They cannot (A. Smith to the contrary) make grimaces or even wrinkle the brow. They can merely stare or droop their lids, move the ears and open the mouth wide enough to expose the teeth.

This lack of facial expression is due in large measure to the immobility of the upper and lower lips. There are two reasons for this condition: 1. the middle of the upper lip is bound by the frenulum to the underlying premaxillary area; 2. the lack of development of the labial and nasal muscles of the facial field. Ernest Huber 1931, (page 23) who has made an exhaustive study of facial muscles of mammals and primates, states that:

"The facial muscles of the Lemur play no role as musculature of facial expression. Indeed we can hardly speak of facial expression in the Lemur."

In common with all other Lemuroidea and many mammals, the galago has a moist, glandular rhinarium with crescent-shaped nostrils, which E. Geoffroy-St. Hilaire (1812) and R. I. Pocock (1918) call strepsirhine. This structure extends into the labial area and becomes the philtrum, or median, attached part of the upper lip. Maxillary portions of the upper lip which are covered with fur may terminate on either side of the naked philtrum as in the case of the lemurs, or, as in the *Galago s. moholi* (Pocock, 1918, and J. D. Boyle, 1932) may meet in front of (over) the labial portion of the rhinarium, a deep groove remaining to show the line of union. In this way the upper lip is completely bounded by fur (Pl. I, Fig. 1).

When the Galago s. moholi is angry and prepared for defense or offense, it opens the mouth so wide that the labial area is stretched and the canines and premolars exposed. There is no ability to draw up the lip in a snarl or to make grimaces of any sort. The enlarged photograph (Pl. I, Fig. 1) of the face of one of the galagos shows the preliminary stage of rage. The mouth is partially opened though not wide enough to show the teeth. The eyes are focused on the cause of irritation located just above its head.

The sense of smell of the galago as of other Lorisiformes is well developed and still serves a more important function than in the higher primates.

Le Gros Clark (page 177) states that:

"In general there is a close correlation between the degree of complexity of the turbinate system and the acuity of smell."... "In Lorisiformes the first ethmo-turbinal is very large and actually covers over the maxillo-turbinal while in Lemuriformes it is much smaller."

The presence of a relatively large olfactory lobe in the brain is additional evidence that the galago and the lemurs, in common with the lower mammals, retain their dependence on the sense of smell.

The galago places great dependence upon its sense of smell. Curiosity is satisfied through this means. Any strange person, or object, is first thoroughly smelled, or food is approached nose first unless it is food-on-the-wing, when it is seized first and smelled afterwards. The facial tactile vibrissae, or "whiskers," around the nose are said to be closely associated with the sense of smell. Though they are not as well developed as in the genus *Lemur*, they are still evident in some degree. The mystacial, mental and genal, are present though more delicate and less obvious (Pl. I, Fig. 1) than in *Lemur*. According to Ernst Huber (pages 22-23), among the Lemurs:

"The mystacial and mental vibrissae jointly with the rhinarium, a highly sensitive patch of mucous membrane at the tip of the snout, subserve the tactile sense of the latter, which is closely associated with the sense of smell. . . . This sense, which plays an eminent role in the life of the primitive, terrestrial mammals, is of subordinate importance in the primates and has already become deteriorated in the Lemuroidea. Undoubtedly in connection with their adaptation to arboreal life, the sense of touch, with the aid of the facial tactile vibrissae, is, however, of the greatest usefulness to these primitive primates in their life amidst the branches of trees. Indeed, the sense of touch together with the highly developed sight and keen hearing are the guiding senses of the lemur."

In my judgment the sense of smell should be added as an important guiding sense.

The mouth and nose of the *Tarsius* are strikingly different from those of the galago or other lemuroids. There are no crescent-shaped nostrils with moist rhinarium extending into the upper lip. Like higher primates, the nostrils are oval and there is only a remnant of the moist area about these apertures, a condition which Pocock (1918) considers of such fundamental importance that in the classification of the primates he uses this feature as a basis for primary subdivision. He calls the lemuroids "Strepsirhini" and all other primates including *Tarsius*, Haplorhini.

d. Eyes.

The large, round eye bulges forward, giving a conspicuously rounded appearance to the surface. In the daylight the entire surface of the eye is colored a homogeneous light brown. Since the whole visible portion of the eye is covered by the rounded, transparent cornea, no portion of the sclera can be seen. The pupil, as A. D. Bartlett (1863) observed long ago in the case of *Galago crassicaudatus montieri*, is vertical (Pl. I, Fig. 1), a condition common to Lemuroidea and to many nocturnal mammals. *Tarsius*, however, differs from the galago in that the pupil is horizontal. A recent photograph which appeared in Collier's Magazine (August, 1939) of Professor John Fulton's two living specimens at Yale University, shows the pupil in the light as a horizontal slit, although in their other respects the eye is strikingly similar.

Under the hand lens, the vertical pupil of the galago eye appears to be slightly rounded at each end and somewhat wider in the center. Fine dark lines radiate from the rim of the slit into the iris. The spacing of the lines seems to vary with the intensity of the light. When the light is bright and the slit narrow the lines seem crowded together. In a dimmer light, the slit is larger and the radiating lines farther apart. A slight scalloping of the edge of the slit between the lines is apparent. At night in a dim light the iris opens to a prodigious extent, leaving only a small portion of the brown visible as a rim. By reflected light the pupil is brilliant orange (like the lemur). The eyelids, which are kept wide open, have lashes on the rims visible on the upper lid of the right eye in the enlargment (Pl. I, Fig. 1). It is difficult to see the lid except when the animals are sleeping. We succeeded in getting a photograph of a form with extended lid after it had been temporarily blinded by a flash-light bulb which it was examining when the light was discharged. The photograph clearly shows the upper lid covering the major portion of the bulging eye (Pl. II, Fig. 3).

The eye is so large that the extrinsic muscles are unable to move it. In compensation the head moves flexibly as a whole in quick motions from side to side and sometimes in an elipse. The head may be bent to the side at such an angle that one eye is placed almost vertically above the other. It may also turn practically 180 degrees so that the nose is directly over the spine and, as Cooke (1939) has noted in the case of the *Tarsius*, the animal frequently moves its head in this manner to look upward. The galago does this when it is clinging to some vertical or inclined branch or when clinging upside down to a horizontal branch. The ability to turn the head in a direction opposite to that which the body "faces," a convenient adaptation for any perching animal, relieves the necessity of lessening the hold on the perch.

e. Ears.

The membraneous ears are large and almost naked on the inner and outer surfaces except at the rim where there is a sparse covering of fur (Pl. I, Fig. 1). The inner surface, as E. Geoffroy-St. Hilaire first and A. Smith later noted, is marked by four transverse ridges which seem to terminate in an outer vertical ridge (Pl. I, Fig. 1). An outstanding galago pecularity is the ability not only to move the ear as a whole forward, laterally or upward, but also to fold the pinna along the ridges somewhat like an accordion, throwing its outer tip back over the upper transverse ridge. In addition to the accordion-like folding, the whole pinna may be further pressed back against the head so that all evidence of large projecting ears disappears.

The ears of the galago are perhaps its most expressive feature. They move singly or in unision in the direction of the least unexpected sound. When looking over a new object or person the ears seem as alert as the nose and the eyes. In sleep there is a tendency to fold the pinnae along the

ridges (Pl. II, Fig. 2, lower center) and in anger there is also some tendency to corrugate them (Pl. II, Fig 2, right). The final flattening of the folded pinnae against the head occurs when the animal enters an enclosed space. When seeking food which I have placed in the cupped palm of my hand, the galago thrusts forward both head and hand, invariably flattening the ears against the sides of the head. This is an admirable device for the protection of large and delicate ears from the dense foliage and perhaps also from the perils of battle.

Tarsius ears, though much smaller relatively, seem to be of a similar type, according to Ernest Huber (page 27), and the musculature which moves them is highly developed.

f. Jaws, Teeth and Tongue.

The round head and short face are characteristic of the several varieties of Galago senegalensis and demidoffii. The upper jaws and the snout with the crescent-shaped nostrils do not project forward to the extent that they do in *Galago crassicaudatus* or in the Malagasy lemurs. The lower jaws, which are also short, bear the usual two pairs of procumbent incisors flanked by the elongate modified canines that project forward almost horizontally and have been known as the "tooth-comb" of the lemurs. The teeth of this incisor-canine complex of the lower jaw converge at their tips so closely that, as M. Russell Stein (1936) points out in the case of the true lemur, the term "comb" is probably inaccurate. "Scraper" is perhaps a more accurate term. The first premolar of the lower jaw has become modified into a somewhat caniniform structure though less so than in the true lemurs. By working against the canine of the upper jaw, this tooth acts as a shearing or a nipping apparatus. The remaining molars and premolars are more advanced than those of the typical insectivorous lemurs as Le Gros Clarke (1934) has recorded, since the† third premolar of the upper jaw is more molarized and the first two molars are quadri-tubercular, having one more cusp than those of the typical lemurs. The two pair of upper incisors, separated by a space in the center, are so small that it has been suggested they are functionless. Because of the strong roots possessed by these teeth in the case of the true lemurs, M. Russell Stein questions this idea. Can these upper teeth function with the lower horizontally placed incisor-canines or can they be used in any other way? I can confirm the statement made by Stein that the upper incisors are functional. The galagos in my possession will frequently bite when handled, and several times the bite has been sufficiently severe to leave a clear imprint of the tooth marks. In each instance the imprints of the upper canines and the two pair of incisors which lie between have been evident, as well as the imprint of the pair of lower caniniform premolars and the scraper itself.

The question of the use of the incisor-canine complex or scraper is an interesting one. In an article published in 1939 on "The Feeding and Grooming Habits of the Galago," I attempted to show that the scraper was used as a toilet or grooming structure. Since then I have experimented further to determine whether, as suggested by Stein, this device is ever used for scraping fruits and biting off leaves. On placing a pear upon the feeding shelf, I found that the scraper was never used. The galago attacked the pear with the canines of the upper jaw and after making a hole in the skin it then inserted its long, thin tongue into the aperture and licked out what it wanted from the interior. Again, when a tree was placed on the porch some of the smaller branches were bitten off. In each case the canines and the first premolars of the lower jaw were used, never the incisors. The general conclusion is that the scraper of the lower jaw, in the case of the galago at least, is essentially a grooming implement though it has not yet been proved that it may not act upon occasion as a food-scraping device.

^{*} Homologous with P₂ of the primitive mammalian dentition.

[†] P4 superior of the primitive mammal.

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The long, thin tongue, like that of the true lemurs, is used for licking and lapping. Although of somewhat limited movement, its action is straight forward over the incisor-canine complex of the lower jaw which acts as a trough. The tongue is long enough to reach the moist rhinarium over which it can curve.

It is interesting to note that *Tarsius* also uses its tongue as a licking and lapping structure.

The Limbs.

a. The Hand and its Action.

It is well known that the fourth digit of the hand among the Lemuroidea is the longest of the five. In this characteristic, they differ from all other primates, including *Tarsius*, and from Mammalia generally where the third digit is the longest. The hand digits of *Galago s. moholi* as a whole are relatively long. The thumb is short and separated from the index finger by a considerable interval; the index finger is also short and separated from the third digit by a less marked interval (Pl. III, Fig. 6). The third and fourth fingers grow progressively longer with the fifth somewhat shorter. The last three digits are more closely placed (Pl. III, Fig. 4).

In 1838 W. Ogilby demonstrated at a meeting of the Zoological Society of London the structural peculiarities of the hand of a living specimen of galago, then known as *Otolicnus garnetti*. This peculiarity consisted in the partially opposable character of the index finger of the hand. It was shown that the thumb and the index finger could be used as a unit to grasp one side of a branch and that the remaining three fingers were used on the other side, much as the koalas would do. Mr. Ogilby remarked, "The anterior index finger in all the 'inferior' Lemuroidea is weak and powerless and it has the same tendency to divide with the thumb instead of with the other fingers in the rest of the galagos as well as in the Nycticebi, the Microcebi, the Cheirogalei, and Tarsii whilst in the Potto it is reduced almost to a tubercle." In watching the action of the anterior digits of the galago, I find that my observations do not agree with Mr. Ogilby's in all respects. The index finger lies almost midway between a large space which separates the thumb from the third finger (Pl. III, Fig. 6) and, in grasping, it is just as likely to be found with the third, fourth and fifth digits as with the thumb. Its disposition depends somewhat on the size of the object grasped. If it is small enough to fit in the space between digits two and three, digit two is then likely to be found on the side of the thumb (Pl. I, Fig. 1); if, however, the object or branch is large, the index finger then lies almost between the two. In any event the index finger is so small that its effectiveness as an opposable structure is very limited.

An interesting feature of the digits of the hand is the size of the individual phalanges of all but the thumb. In each instance the proximal phalanx is long and the second one is slightly less so while the third or distal phalanx is minute and very little larger than the nail. The relative length of the phalanges is an admirable adaption for grasping limbs and small branches of trees. Two peculiarities, however, are evident because perhaps of the elongation of the proximal elements. 1. When the galago places its hand upon a flat surface, the palm of the hand with its pads rests flat upon the surface; the digits, however, are not extended straight forward but are flexed, the pads on the distal ends of the digits alone resting upon the surface. There seems to be a flexure at the knuckles which permits the raising of the proximal phalanges away from the ground. Furthermore, the joints between the first two phalanges instead of pointing directly upward are bent to the side, even the index finger may be involved (Pl. III, Fig. 4). A recent motion picture of Dr. John Fulton's live *Tarsius* shows the same flexed condition of the digits when the hand rests upon a flat surface. 2. A

second peculiarity is to be noticed when the galago grasps a piece of food. Among the other primates the digits flex over the object at the knuckles and the palm of the hand is involved. In this instance, however, the proximal phalanx of each digit (the longest) remains straight on a plane with the back of the hand, and the grasping is done by flexing the two distal phalanges over the proximal. The thumb acts in opposition and the palm is not covered by the digits (Pl. III, Fig. 5).

b. The Foot and its Action.

The enormous hallux of the foot is widely separated from the other four toes which act as a unit (Pl. III, Figs. 6, 7; Pl. IV, Fig. 8). The fourth digit, in this instance like that of *Tarsius*, is again the longest of the five, while the second toe is short and, as in the case of all other lemuroids, bears a flexed claw (Pl. IV, Fig. 10). All the other digits of both hands and feet have nails which are flat with relatively straight edges (Pl. III, Fig. 4) (A. Smith, 1836). The great distinction of the foot of the galago as compared with other lemuroids is the extraordinary elongation of the navicular (scaphoid) and the calcaneum first noted by E. Geoffroy-St. Hilaire. The digits and distal portion of the metatarsals are the only elements which rest upon the ground. The proximal portion of the metatarsals are well as the tarsals are always off the ground; in fact, as Pocock (1918) has admirably shown, the ventral aspects of this area of the foot are covered with fur and are usually raised some distance from the ground (Pl. III, Fig. 7; Pl. IV, Figs. 8, 9). The total length of the foot is 2 to $2\frac{1}{4}$ inches, about half the length of the hind leg. It is this unusual lengthening of the tarsal segment which makes possible the extraordinary leaps characteristic of this form.

c. Volar and Solar Pads.

The well developed pads on the palm and the sole of the galago are quite primitively disposed in a characteristic manner (Pl. III, Figs. 6, 7). There are two proximal pads, the thena and the hypo-thena, and four distal interdigital pads. In both hand and foot the thena pads tend to fuse somewhat with the first interdigital and the hypo-thena with the fourth interdigital. The interdigital pads of the foot are not all of equal size, the third being much smaller than the others.

Pads also are to be found on the toes and fingers (Pl. III, Figs. 4, 6, 7). Along each digit between the palm or sole, and its tip, a long, thin pad is found which enlarges at the tip. Although this enlargement or pad is not equal in size to that found on the tip of the *Tarsius* digits, it is, however, an effective surface. The big toe has a broad distal and proximal pad. The first interdigital which follows is a round, conspicuous pad, protruding beyond the confines of the digit and the sole (Pl. III, Fig. 7). Oblique papillary ridges are to be seen on the pads. Dr. Charlotte Wolff (1938) has found "unique scale-like roughness" in two species of galago (moholi and crassicaudatus) as well as in *Loris* and in the genus *Lemur*. She describes them as more expressed on the sole than on the palm and are found in the center of the palm and sole and on the lower phalanges but not on pads. She also finds that all the terminal phalanges have tactile corpuscles.

d. The Hind Limb and Its Action. aa. Climbing. bb. Moistening of Pads. cc. Jumping.

Not only is the hind limb very long, but its strength is also enormous. The animal can hold on by its hind feet alone (Pl. IV, Fig. 9); it can lower itself down into a jar, or suspend itself freely, head downward. By the power of the muscles of its hind legs, combined with the strength of the muscles of the foot, it can lift itself once more to its original position without the aid of the anterior limbs. One of the tamer individuals born in captivity will

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grasp a finger of my hand by the huge opposable big toes and the other digits of its hind feet and will let itself down into a paper bag suspended from my hand. The strength of the grasp of the large toe and the other digits upon my finger seems out of proportion to the size of the animal. There seems also to be a particular pressure exerted by the hallux and the inner surface of the sole of the foot. This is the area where the interdigital suction pads are especially well developed. The added pressure exerted at this point flattens out the adhesive pads and makes them more effective as a clinging device. The use of the pads as an aid to clinging is shown in the illustration (Pl. III, Fig. 6). This photograph was taken from the inner side of a glass door on the outer side of which the galago was clinging. The pads of the hind feet press against the flat surface of the glass, obliterating the spaces between the pads and show the way in which the large pads of the big toe and the first interdigital adhere firmly to the glass surface. This explains the animal's ability to climb up and down any perpendicular surface which offers an edge, such that the thumb and great toe can get a purchase. The galago always descends head first.

Grasping and climbing are facilitated not only by the elongation of the fourth digit over that of the third and by the strength and opposability of the very large, widely abducted hallux, but also by the moistening of the pads of both hands and feet. The latter action is one characteristic of the galago which is accomplished in a definite way at frequent intervals throughout the active period, whether climbing or sitting still. By placing the palm of one hand under the urethral aperture, the animal collects a drop of urine. It then rubs the moistened palm of the hand on the sole of the foot of the same side, repeating the action with the other hand and foot. This automatically moistens the naked surfaces of the pads and renders them more effective surfaces of adhesion. No one seems to have recorded this action except E. G. Boulenger, who, in his popular book, "Apes and Monkeys," states that the galago has "a strange habit of moistening the palms of the hands and the soles of the feet at frequent intervals when climbing" (p. 206), although he gives no clue as to the way in which this is accomplished, nor does Mr. Boulenger record this as a common practice even when the galago is sitting quietly.

The galago, essentially a hopping and jumping animal, normally perches in high places (Pl. IV, Fig. 8). Although it uses all four feet for climbing and usually for perching, it does not normally run or walk on all fours. The structure of the posterior limbs is responsible for the characteristic hopping and leaping motions. When jumping on a horizontal plane this form can span as much as six feet. Vertically it can spring upward as much as five feet, landing on a perch with unerring precision. When jumping downward diagonally from a higher to a lower perch much greater distances are covered.

As an example, one of the adults sprang from the balcony rail of a studio room to the top of an open door in the room below, a distance of twenty feet. Although the thickness of the door was only two inches, the landing was made with precision. When, and rarely, the adult galago makes an imperfect landing, it seems to be due to an insecurity of grasp rather than inaccuracy of gauging distance. The speed and extent of the jump is particularly great in this variety and exceeds that of the larger species (crassicaudatus).

The preliminary stages of jumping are expressed by a crouching of the body. The hind feet are placed with heels together off the ground and toes out. The spring is made with great speed and the feet are kept in the same relative position as attained when taking off, though somewhat farther apart. From a front view of the approaching animal the soles of the feet can be seen slightly up-raised. The heels are no longer touching, but may

remain relatively close together. This explains the ability of the galago to jump even though his legs are bound together above the heel. Donald Carter, in his field notes of his trip in South Africa (1938), recorded the following:

"Balovale, September 4.—A native brought us four (two males and two females) galagos alive in a gourd. Upon removing the wad of grass which served as a plug for the hole, one of the animals jumped out landing on the table. From there it jumped a good six feet to one of the posts supporting the tent and without a moment's hesitation he took another jump to the trunk of a small tree under which the tent was pitched. This jump must have been eight feet. Up this tree he scrambled and hid among the boughs, I sent a boy up the tree and with some difficulty the animal was dislodged and jumped to the ground where he was pounced upon by about five small boys who were waiting underneath. It was not until he was retrieved that I noticed that the animal had his two hind legs securely tied together at the ankles by a piece of grass. Hampered as he was he easily and gracefully made these two jumps landing both times where he had planned."

Before taking off to a new position the eye of the galago always gauges the distance to be covered quickly and carefully. The jump to a new perch may involve a diagonal or backward leap. The animal, however, always manages to face the new perch on landing, though it may mean a 180 degree turn in mid-air.

Occasionally the galago will stand up straight, balanced on its toes with the hind limbs not flexed. In such a position, it immediately becomes quite tall (11 inches) and of a short-waisted appearance because of the relative length of the hind legs and feet (Pl. IV, Fig. 10). The tail, from eight to ten inches long and somewhat bushy at the end, serves as a balancing structure when jumping or when standing upright. In the latter action the tail moves up and down to help maintain balance. It may also serve to protect the eyes from the light while sleeping, though it is more frequently curled over the breast at such times. While the tip of the tail continues to be slightly curled when the animal first awakens, it straightens out as soon as the galago becomes active.

The Reproductive Organs.

R. I. Pocock in his admirable article, "On the external Characters of the Lemurs and Tarsius," (1918) has described in detail the structure of both male and female reproductive organs of *Galago senegalensis*, crassicaudatus and montieri as well as other forms of the Lemuroidea. The presence of baculum and spines on the penis seems to be a condition common to all male Lemuroidea but invisible of course in the living state.

The male in conformity with the lemuroid type (except the genus Lemur) has an external scrotum covered with fur. The penis is relatively short with a long, inverted tip. Recently, just before the period of heat of the female, (December, 1939) I saw the everted tip of the penis. Its shape differed from those described by Pocock for crassicaudatus, senegalensis and demidoffii. The everted portion was a relatively narrow cylinder, over an inch in length, which expanded suddenly into a wide bulb at the tip. As I watched, the bulb suddenly contracted with startling speed to almost the dimensions of the rest of the penis. As I was fully six feet away from the cage when I saw this structure, it was not possible to see whether the bulb after contracting formed a structure comparable to the "frill" which Pocock described as present in the case of the tip of the penis of Galago crassicaudatus.

The female *Galago s. moholi*, as Pocock has shown in the case of galagos of other species, possesses a long, pendulous clitoris, at the terminus of which is the urethral aperture. This peculiarity makes it difficult to determine the sex of the individual as the structure resembles superficially a penis in shape and length. The inverted tip of the penis and the presence of the permanent scrotum, however, differentiate the male.

DISPOSITION.

The galago is a very quick and nervous animal, which responds to the slightest unexpected noise or movement. It will crouch in terror and then spring away from the direction of danger with lightning speed. Like most lemurs, though easily tamed, it is somewhat truculent and uncertain in its relations to humans. It resents handling. Balancing on its haunches, it will hurl itself forward, striking out first with both hands like a diminutive prize fighter, and then grabbing hold of the object. Since the nails are flat, this is a harmless gesture. But this attack is followed by a quick forward thrust of the head and a very nasty bite may be inflicted by the sharp canines and the first premolars of the lower jaw. At times even the scraper is involved. During the attack the animal utters a querulous chatter. The truculence of the galagos seems to be directed solely toward humans. I have never seen them fighting among themselves. Even the young ones are independent and dislike handling, though they will tolerate a gentle rubbing of a finger along the jaw or behind the ears. The presence of several people does not disturb them providing no quick movement or noise is made. Completely fearless of humans, the twin galagos born in capitivity enjoy jumping on a shoulder or sitting on the top of someone's head.

The galago is as inquisitive as a monkey. Unlike that animal, however, curiosity manifests itself by smelling instead of handling the strange object. The galago will investigate the face and wearing apparel of even a total stranger. Anything new brought into the cage or enclosure is always smelled carefully.

I have attempted to show in another article (1939) that Galago crassicaudatus, when alone, and dependent upon humans for companionship, was a relatively affectionate animal which treated me much as it would a fellow galago. Without doubt the Galago s. moholi would be more demonstrative to humans were it dependent on them for companionship. It cannot be said, however, that this group of four display any real affection beyond their own circle. Their interest in me, I suspect, is due to the food I supply. As a group they play together in utmost harmony. They will pursue each other, roll about, and playfully grapple. At times they will hang suspended from a horizontal stick by their hind feet the while beating at each other with their free arms like two inverted pugilists. At feeding time it is a question of each galago for himself, although when the babies were beginning to eat and for a few months thereafter, their mother would sometimes give up part of her catch to a hungry young one who had jumped up beside her to help itself. Food in the possession of other galagos is much more attractive than any food in a plate. They will spend a great deal of time pursuing succulent morsels in the hands of one of their companions, even though similar morsels may be present for them. There seems to be no resentment on the part of the pursued if its prize is taken from it. The galago immediately proceeds to recapture the diminishing tid-bit.

BEHAVIOR OF THE ADULTS.

Although the behavior recorded in this section has been observed while the galagos were in the state of captivity, nevertheless the conditions under which they were kept have approximated, so far as is possible, their natural environment. Hence, I am justified in feeling that this general behavior does not differ fundamentally from that of the wild state.

Feeding.

Observations of this variety of *Galago* confirm the recorded statements that while they are insectivorous, they eat other things as well. Live moths,

grasshoppers and meal worms are great favorites. Milk, a constant in their diet, has never been refused. Vitamin B and cod-liver oil have been added occasionally to milk, especially after the birth of young. Sweetened fruit juices and melted ice cream are relished. Although water has frequently been placed before them, there is no evidence that they drink it. They will eat various kinds of thinly sliced raw vegetables and fruits at any time; more freely in the winter months when insects are difficult to obtain. They will also eat buttered bread or bread spread with honey in which wheat germ meal and rice coating flour are mixed. When cut flowers from the garden are available, such as bergamot and honeysuckle, they will bite off the heads, pull apart the petals and chew at their bases.

In the case of live food, as Geoffroy (1796) first recorded, the galago fixes its gaze intently on the insect. It never attempts to jump at it in midair; instead, it leaps up to a perch close beside the insect. Then holding on with its hind feet, the galago reaches out and grabs the moth with one or both hands. After putting the live moth in its mouth, it jumps away to a secure perch somewhat removed from its companions. Sitting up and holding the insect in one or both hands and closing its eyes to protect them from the frantic beating of the insect's wings, the galago begins at the head and consumes all but the wings. This is the same procedure which Cooke has recorded in the case of the *Tarsius* (1939). The wings are discarded by using the tongue to shove out over the scraper, which thus seems to be passively used as a trough. I have frequently placed moths in a wide-mouthed jar covered with a loosely fitting lid. The galagos quickly learned to push off the lid by using the tip of the nose. Standing up, stretched to full height, one will peer in and leap to the rim with all four feet bunched together. Then liberating the front legs but still holding on with the hind feet, the galago will dive in head first, locate and grab the insect with one hand and haul itself back by the power of its hind legs without loss of balance. Even when there is plenty of food flying about, the galagos tend to grab it from each other.

Vegetables and other inert food are always smelled carefully before sampling. If acceptable, the animal takes a small piece directly in the mouth, jumps away, and holding the morsel in one or both of its hands, bites off what it wants and drops the rest. Liquids are usually lapped up by the long tongue; at times, however, the hand is plunged into the fluid and subsequently licked dry.

Feeding takes place regularly. In the morning milk is placed in a shallow container close to the sleeping box. By the end of the day most of this has disappeared. At about 8 o'clock in the evening various foods and a second supply of milk are provided and left available throughout the night. The animals which have been active for some time are now hungry. They rarely consume a whole piece of vegetable or fruit; their habit is to take a few bites and drop the rest. In the morning the enclosure is strewn with fragments.

Throughout their active period, fecal elimination is very plentiful; the more so when they first become active at night. Urinary elimination is also plentiful and frequent, and usually independent of moistening the foot-pads, which has already been described. Though they rarely soil their sleeping box, they seem to have little further concern about the place for elimination. If handled during the day, they express fear or nervousness by immediate urinary and fecal elimination.

Grooming.

The galago is an unusually clean animal. Even its hands when solled by food or foreign substance are carefully licked clean. General grooming involves the frequent use of the procumbent scraper, the tongue, and the occasional use of the claw which serves as a scratcher for such spots, otherwise inaccessible, as behind the ear.

The chief grooming instrument, the procumbent scraper, long called the "comb," is used by the galago in vigorous action on his own pelt or on that of one of his companions. This action is a series of quick thrusts through the fur deep down to the integument. By this scraping action the animal can dislodge and remove any dead skin or foreign substance in the pelt (Lowther, 1939). The tongue completes the process of grooming with a thorough gentle licking.

Begun on first awakening, before the start of much activity, the grooming is repeated for short periods frequently during the active period. Grooming may be a mutual operation. I have seen two galagos grooming each other simultaneously; and two young ones may work on one of their parents at the same time. As for the action of grooming on the part of a galago of another species (*crassicaudatus*) with no companions other than myself, I have had personal experience. This animal frequently perched on my arm or hand and vigorously dug into my integument with its scraper as though I were a fellow galago. The intensity of the digging and scraping made it clear that any foreign object in the fur of a galago could be effectively removed. While the present variety of galago has not bothered to attempt much grooming of their mistress, the young ones occasionally have repeated the action of the former galago, particularly after licking off some sweet morsel adhering to my fingers. At times they have used the scraper perhaps to get off the last remnants of sweetness.

Calls.

The galago has several notes characteristic of different conditions, clearly differentiated but difficult to describe. 1. The alarm note; a shrill sound on a high pitch, which starts somewhat like a chipmunk's scolding note, though shriller, but which ends in a whistle. This note quiets the group into frightened stillness. 2. An automatic cry, the cause of which is unknown, and which may continue for an hour. It is a piercing noise with two pitches, high and low. While the animal is making this noise it will continue its activity, eating and jumping. It does not affect the others. 3. The low clucking note like the brooding hen, but on a lower register; used when annoyed. 4. The sex note, used by the male when pursuing the female. This is a soft questioning sound of two notes. 5. The conversational note; when separated, both male and female call to each other. This note is softer than the sex note but has the same two pitches, high and low. 6. A chattering note used by the female as an expression of annoyance at the attention of the male. 7. The maternal note; a very gentle, soft, caressing sound, used by the mother when talking to the young in the nest. 8. The squeak of the young; suggestive of young mice. It might possibly be called a squeaky chirp.

Sex Behavior.

The female of this form will accept the male only during periods of oestrus, which may last as long as five or six days. At this time she has a colorless discharge which perceptibly excites the male. He constantly smells her genitalia and just before the act of copulation the male is likely to lick the female with his long tongue. During the period of sex activity copulation has been observed to occur three or four times a night and it has also been seen in the morning when the animals would normally be sleeping. During the long periods between oestrus, the male continues his interest, although the female refuses to accept him. As he pursues her around the cage or enclosure, he utters a soft, plaintive call which I have described as the

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"questioning sex note." At times the female merely keeps one jump ahead of the male and seems undisturbed by his attentions. If, however, they are continued for any considerable time, she finally turns upon him in annoyance with a chattering cry. This usually effectively discourages his attentions. Once, however, I saw the female become so angry, after chattering at the male without effect, that she turned upon him with such fury that he took to his heels in alarm. Generally speaking, the adult pair is a friendly and affectionate couple. They are frequently found perching side by side, grooming each other, wrestling and at times embracing (rubbing noses). During the period of pregnancy the female's disposition became far more truculent. The continued attentions of the male were repelled with increasing vigor and shortness of temper.

Nesting Habits.

The galago in the wild is in the habit of nesting in the hollow places among the tree-tops, according to E. Geoffroy-St. Hilaire, Pitman, Shortridge, and others.

E. Geoffroy, 1796:

"Ils nichent dans des trous d'arbres où ils préparent à leurs petits un lit qu'ils tapissent d'herbes."

Pitman, 1934:

"I have often come across the leafy beds these animals prepare for expected offspring at the bottom of hollows in trees."

Shortridge, 1934:

"Galago moholi granti is strictly nocturnal, sleeping during the day in hollow trees where it may generally be taken in small family parties."

In captivity, I have found that these animals show a tendency to tear up bits of available paper and to carry them into the sleeping box. While on the porch where a growing apple tree is situated, they bit off the ends of leafy twigs and carried these to the box up under the eaves of the porch roof. They would also gather bits of string, wool, heads of flowers and almost any other small soft object which happened to be loose. Just before the birth of young ones, the female was particularly active about the construction of a lining for the sleeping box. The galagos obviously prefer a darkened area in which to sleep during the day. Whenever a box was given them they used it rather than some secluded corner of the cage or porch.

F. Wood-Jones, p. 116 (1929) states that:

"Nest-building is a habit that is widespread among the Lemurs, and it occurs both in the species found in Madagascar, and in those living in continental Africa and in Asia. The curious Aye-Aye "Chiromys" builds an elaborate nest which has been described by Baron as a structure about two feet in diameter and entered by a hole in the side. Shaw has described the nest of "Chirogale milli" as consisting of "leaves and Dry Grass," and that of "Microcebus smithii" as resembling a bird's nest."

BREEDING SEASON AND PERIOD OF OESTRUS.

Galago Activities.

When received in September, 1937, the female was immature. Ten months later (July 19, 1938), she experienced the first onset of oestrus. She did not become pregnant, however. After an interval of five months a second period of oestrus occurred (December, 1938) which resulted in the birth of twins four months later (April 14, 1939). Oestrus did not re-occur until

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December 10, 1939, although the young stopped nursing sometime in July. At intervals of six weeks three additional short periods developed, and a fourth occurred twelve weeks later. A table of these data follows:

	Length of oestrus	Result
Female matured July 19, 1937	5-6 days	no fertilization
Second oestrus Dec. 15, 1937	5-6 days	twins (born Apr. 14)
Third oestrus Dec. 10, 1939	at least 3 days	no result
Fourth oestrus Jan. 22, 1940	at least 3 days	no result
Fifth oestrus March 7, 1940	?	no result
Sixth oestrus May 29, 1940	3 days	no result
** Oestrus recurred Dec. 7, 1940.	See Appendix, pag	e 461.

The only conclusions which can be drawn from these limited data are: 1. the period of gestation is four months; 2. a restricted season of sexual activity is indicated. Whether December normally initiates the sexual season in the wild state and the first expression of oestrus in July was atypical, or whether the latter is typical and the shift from July to December is an adaptation of the animals to their new environment, cannot be determined. In any event this evidence still indicates the time for the birth of the young is limited to the period between April and November. 3. It is also evident that like many other forms with a limited breeding period, in the absence of fertilization oestrus will reoccur at intervals, thus establishing the galago as poly-oestrus within the limits of their sexual season.

Comparison with Breeding Habits of Other Lemuroidea.

Zuckerman substantiates the conclusions that the moholi galagos, like the lemurs, have a restricted breeding season. He states that although the records are too few to place any definitive reliance on them, they nevertheless indicate that the breeding season is betwen April and September, with the majority of births taking place between April and June. He bases these conclusions on the record of seven births of *Galago s. moholi* which have occurred in the London Gardens between 1856 and 1927.

Donald Carter, mammalogist of The American Museum of Natural History, who recently returned (1938) from an expedition in South Africa, has made available to me his field notes and many specimens of *Galago s. moholi*, most of which were taken at Balovale, Northern Rhodesia, on the Zambezi River.

Between August 23 and October 15, Mr. Carter secured more than one hundred adults of which he brought back seventy-two to the museum. Two of the 29 females contained embryos, and one he noticed was nursing young. (He tells me that he did not record whether the remaining females were nursing). In addition to the adults 20 young galagos were brought into camp by the natives. The following is a digest of Mr. Carter's field notes concerning the young taken at Balovale:

August 23 1 pair shot, female nursing young
September 4
September 14 1 female with two fully formed embryos
September 18
September 201 young
September 24
September 26
September 27
September 282 young
October 12 young
October 102 young
October 15

An analysis of these data reveals that:

- 1. The relatively uniform dimensions of the adults indicate that they were at least a year old.
- 2. A comparison of the pelage and measurements of the young in the museum collection with those taken during the growth of the pair in my possession shows that the largest were not more than four or five weeks old.

Zuckerman (1932) states that three births among Galago garnetti occurred, one in May and one in June, 1930, and one in September, 1929, in the London Gardens. This corresponds with reports of births in the London Gardens among the true lemurs where only very exceptionally were there records of births outside the period March to June. Zuckerman states that, "All the sixty-six births occurring in the London Gardens Zoo were distributed in the period March to September, sixty-four between March and June, and two in September." Major S. S. Flower (1933) presents additional data which "provide a very good reason for arguing that species belonging to the genus *Lemur* have a demarcated breeding season. The following table showing the months in which 120 lemurs were born in the Giza Zoological Gardens confirms Zuckerman's opinion":

March	births births births births	${f Twins}\ 3$	Triplets 1

120

From this additional evidence it is conclusively established that the galago, like the lemur, has a restricted breeding season ranging from April to October, but that probably the galago south of the equator is more apt to have young in September and October than the lemur.

Zuckerman (1932) states that, "The breeding habit of the African members of the series Lorisiformes appears to be different from that of the Asiatic species belonging to the same subdivision of the Lemuroidea. Thus, the few available records regarding births in the genus *Galago* suggest that the animals belonging to this genus may have a restricted season, whereas the Hubrecht data for the slow Loris (Nycticebus coucang) prove that this animal breeds throughout the year." According to him, however, its curve of fertility seems to rise toward the end of the year.

Discussion of Environmental Causes of Oestrous Change.

An interesting article written by F. H. A. Marshall (1937) presents evidence that the reproductive rhythm may be influenced by extero-ceptive or other environmental influences, and that the oestrous cycle may be reversed in animals living in temperate climates after transference across the equator. He concludes that "among the insectivores, carnivores, rodents and nonruminating ungulates with very few exceptions outside the tropical areas breed in the spring or first half of the year in the Northern Hemisphere." Also, "That they react to seasonal changes in a remarkable way is shown especially by those natural experiments in which animals of various species that normally breed once annually have crossed the equator and as a consequence have been induced to have two sexual seasons in one year." Marshall emphasizes the potency of more or less light as an activating factor. He further states that "Tropical and subtropical forms, however, such as antelopes (red and blue duiker) which live under comparatively uniform conditions as regards daylight, may have an extended breeding season or breed

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all the year. They do not adjust themselves to the changing conditions of temperature in regard to sexual activity."

Following this analogy, could not the differences between the breeding habits of the lorises and the galagos be accounted for by a study of differences constant in their normal habitats? Since all these forms are nocturnal and tropical or subtropical, the value of more or less light as a breeding factor is not as important as conditions insuring a constant food supply, or other environmental influences. The *Galago senegalensis moholi* and *Galago* crassicaudatus and their subspecies live in the open savanna country where there is a prolonged dry season lasting from April through October, during which their young are born. The lorises, however, live in forested tropical regions where there are no such extremes of humidity and dryness and where a restricted breeding season would have no survival value. It would be interesting to determine whether *Galago demidoffii*, a small form found in the rain forest of Equatorial Africa in the very regions in which the duikers, cited by Marshall, live, would, like them, have continuous or irregular breeding season as a result of more uniform environmental conditions.

PERIOD OF GESTATION.

As I have reported, the first period of heat, experienced by the young female under my observation, was not followed by pregnancy. The second period, however, which began five months later, proved to be a fruitful one. No peculiar conditions were noted for two months. The female then displayed increasing irritability at the attention of the male. She showed preference for the warmth of the radiator at the corner of the room and gave up jumping to high places. Her pelt became patchy between the shoulders. She looked thin and in bad condition. During the third month the female's irritation at the attentions of the male was so great that I separated them, giving each a cage. Paradoxically the female would answer the male's conversational note and seemed to enjoy talking to him from a safe distance. She showed enormous interest in food, eating very much more than usual, and seemed particularly fond of buttered bread. Since she refused cod-liver oil in milk, I smeared it on her fur, so that in licking it off she acquired an adequate dosage. During the intervals when both were liberated for exercise, the truculence of the female increased. A week before the birth of the young the female became very active in building a nest in her sleeping box. Tearing up pieces of newspaper, she carried them into the box. On the nights of April 12 and 13, 1939, she was unusually active.

BIRTH AND NUMBER OF YOUNG.

On the evening of April 14, I opened the doors of both cages to give the animals their customary exercise. The female was still in her sleeping box. On returning to the room a half hour later, I found her perched on the edge of the cage, holding in her mouth a dangling infant. All the while she was uttering a strange, protesting cry, directed at the male who had entered her cage and was watching the scene attentively. Obviously disturbed at his presence, the female jumped out of the cage onto a portiere and from there to the picture molding, her young one still clutched in her mouth. She finally made a downward leap of fully ten feet onto the bed, and from there retired to a dark corner of the room where she deposited the squeaking infant. I found a second young one clinging to the perpendicular side of the cardboard sleeping box. I cannot say just when the young were born. The pelage of one seemed still wet. The box was clean and there was no evidence of the placental membranes, which must have been eaten by the mother. The birth of twins among galagos of this species seems to be a common occurrence, although single births do occur.

Donald Carter's field notes indicate that two young are frequently found in a nest, and Shortridge (1934, page 00) states:

"Twins seem to be of frequent occurrence. In Northern Rodesia---Ndola----several females were found carrying twins."

"A female in a Pretoria Zoo suckled two young ones. Another female gave birth to two young in October."

Haagner (1920, page 10) states that two is the usual number at a birth. There have been other instances, however, of gravid females containing but a single foetus.

Other galagos such as *crassicaudatus* and *crassicaudatus monteiri* are more likely to be carrying single foetuses (Pitman, 1934, page 159). This resembles more closely the habit of the Malagasy lemur where, as the statistics show (S.S. Flower, 1933) (*vide supra*, p. 451), among 120 births there were but three instances of the birth of twins and but one of triplets.

POST-NATAL CONDITION OF THE YOUNG.

The young, male and female, were about the size of my index finger, and almost as slender. Their eyes were partly open. The tail was curled in a loose spiral, and they were sparsely covered with a homogeneous gray pelt.

The fact that the infant galagos were able to cling to the perpendicular surface of the box, and actually to stand on all fours shortly after birth, is of interest.

The young creep about, and after the first day or two of clinging to the mother with all four feet, they may be found under her, feeding, or in the nest. While they never cling to the parent as she moves about, frequently they will climb on her back or creep between her legs when she is crouched quietly in the cage. (Pl. VI, Figs. 15, 17). When in motion, however, they are either left behind, or she picks each up in her mouth, by the neck or the back, much as a cat would her kitten, and carries them about one at a time (Pl. V, Figs. 11, 12, 13). The passive infant accommodates itself to this treatment by drawing up its legs close to the body (Pl. V, Fig. 12).

Donald Carter reports that the young *Galago s. moholi* brought in by the natives were found in the nests and never found clinging to an active parent. These observations are at variance with those recorded by Shortridge (1934) and Haagner (1920) in the cases of captive animals in the Zoological Gardens of South Africa. Shortridge states:

"The young cling to the under side of the mother and are carried about in this manner until more than half grown, the mother being much hampered in her movements, when the young become larger."

Haagner states (p. 19):

"They cling to the mother like the young of the ordinary Ringtail Lemur and South American Marmosets, and ride on her back or hang underneath her as opportunity offers."

These statements by Shortridge and Haagner imply that the mother jumps about with the young clinging to her ventral surface or her back. Careful observation of the family under discussion has never disclosed any such action. When feeding the young are on their backs on the floor of the cage and the mother remains quietly in one position. To be sure, the young do cling to the under surface of the mother by their front legs, but the hind legs are always free and protruding beyond the body of the mother. They may also be found sitting on her back (Pl. VI, Figs. 15, 16) or later on the father's back, but this is only when the animals are quiet or sleeping. There never is any clinging action (as Haagner has suggested) such as one finds among the monkeys when the parent is active or jumping about. Shortridge's statement about the mother's being much hampered in her movements is misleading. She obviously could not move when the young were nursing, and during activity they were never attached to her in any way, unless she decided to move them by carrying them in her mouth.

In contrast with these findings, however, F. Wood-Jones⁵ and P. L. Sclater⁶ both describe the mother of the genus Lemur as the passive agent, the young clinging to the ventral surface of the parent, and using its own tail to help hold itself on to the parent body. The young lemur therefore is the active agent.

Hill, in 1937, described the birth of twins of the slow loris (Nycticebus *tardigradus*). He writes that the young are sturdy and that the mother placed them on the ground at the very beginning. He does not state how the mother carried them about, but implies that she does the carrying, and the young are passive.

Hill, 1937, page 388:

"She will rush toward the baby and pick it up if danger threatens, and place it down again when the risk is over. She will leave her food to do this. If the baby is marooned, it squeaks for its mother, and she will try to get to it, if she is able. If the baby is picked up for observation and replaced, she has not dis-carded it, but smells it, licks it clean, and allows it to go to sleep again."

Cuming, in 1838, described the habits of a Tarsius with her young which seems to have a striking similarity with Galago s. moholi. He states that the young when born have their eyes open, are covered with a good pelt of fur, are able to creep around the cage shortly after birth, and the parent carries the young around, in the mouth, just as in the case of Galago s. moholi.

H. Cuming, 1838, page 68:

"The young appeared to be rather weak, but a perfect resemblance to its parent; the eyes were open, and the body covered with hair; it soon gathered strength, and was constantly sucking betwist its parents legs, and so, well-covered by its mother, that I seldom could see anything of it but its tail; on the second day it began to creep about the cage with apparent strength and even climb up to the top by the rods of which the cage was composed. Upon persons wishing to see the young one covered over by the mother, we had to disturb her, upon which the dam would take the young one in its mouth, in the same manner as a cat, and carry it about for some time; several times I saw her when not disturbed trying to get out of the cage, with the young one in her mouth as before. It continued to live and increase in size for three weeks, when unfortunately some person trod upon the tail of the old one, which was protruded through the cage, a circumstance which caused its death in a few days; the young one died a few hours after, which I put into spirits."

Le Gros Clark (1924), however, does not corroborate this observation with relation to the Tarsius. He states that:

"I have kept under observation several female Tarsiers and young and have never been able to confirm this"... (carrying of the young by mother in mouth). "The young cling to the fur of the mother's abdominal wall, grasping with both hands and feet, and are not in any way held by the mother. In this way the little animal is very often wholly concealed from view when the mother is in a resting position, clinging to a branch"—He further states that: "At birth the Tarsier has reached a comparatively advanced stage of development. The eyes are open, and though its movements are uncertain, the animal can cling to a vertical branch, and scramble about the branches in a hesitating way. When disturbed it assumes an appearance of alertness."

⁵ Wood-Jones, 1929, page 115. "Lemurs do not nurse or handle or carry their young ones, for it is not the mother that clasps the offspring, but the offspring that grips the mother." ⁶ P. L. Sclater, 1885, p. 672. "Young lemur lies nearly transversely across the belly of its mother, and, passing its long tail around her (mother) back and so on to its own neck, uses it as a prehensile organ to hold on by."

NURSING AND CARE OF THE YOUNG.

The female has two pair of mammary glands. Those of the anterior are so laterally placed that each lies practically on a line with the inner border of the arm. The inguinal pair lie closer to the median line. During the first two days the young clung to the mother by all four feet. I saw one nursing from a pectoral mamma while its body was attached transversely under the mother's arm and around onto her back. Within a few days, however, they began to stretch out on their backs in the nest, gripping the mother with their front feet, while their hind feet protruded grotesquely from under her body. Occasionally they would give a convulsive kick. At first the young were so small that the mother had no difficulty in covering all but their protruding legs with her own body. As they grew larger, however, she was obliged to lift herself more and more to accommodate them, causing her front legs to be bowed over them in a ludicrous fashion. Finally they grew so large that she could accommodate only one at a time.

During the period of nursing, which lasted three and a half months, the mother displayed an enormous interest in food. Her consumption of milk was more than twice as great as before pregnancy. And she would now even tolerate in it cod-liver oil, which perceptibly improved her pelage.

The mother kept the young clean by grooming their fur herself. At their nursing time, while they were lying on their backs, with hind legs extended, she would lick clean their genitalia.

During the period of nursing the mother's urine carried the odor of sour milk.

PARENTAL ATTITUDES.

The mother galago displayed great solicitude for her young. When they were taken out for inspection, she would go to the length of jumping close to and even brushing my arm in her agitation. When the young were put down, she promptly gripped one in her teeth by the neck and jumped to the cage, using the pendant youngster instead of her nose to lift the cage door. Having recovered one infant, she then proceeded to rescue the second, in a similar manner. A thorough licking and smelling of the young followed their return to the nest. During the first three weeks the male was kept in a separate cage except during the periods of exercise. He seemed restless and curious about the occupants of the other cage, eating relatively little and keeping his eyes glued on the activities across the room. When liberated for exercise the male invariably made his way to the cage and tried to open the then locked door. The mother, permitted to exercise with the male, seemed glad of her freedom and was willing to play to some extent. When the young were three weeks old the galagos were all placed in the same cage without ill effects.

Perhaps the separation of the parents was an unduly cautious move, but the circumstances seemed to warrant this action. For the first few weeks the mother made very soft caressing sounds to her young and they were frequently heard making small mouse-like squeaks. As the infants grew, the mother continued and the father assumed solicitous attitudes, and even up to the age of nine months they obeyed the call of the mother. During the summer months when the family occupied a screened-in porch, I often heard and watched the mother give the signal for the hour of retirement after a night's activity. Just before sunrise, she would start a soft, conversational note and the young as well as the mature male would answer her call and immediately jump to her side. Within five minutes all four would have retired into the sleeping box for the day's rest. The action of the mother indicates a greater sense of responsibility toward the young than that of the father. It is she who warns the group of any danger. When a

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cat lurked on the steps leading to the porch, it was the mother who gave the alarm call ending in a shrill whistle, which warned the family and sent me on a tour of investigation. In the winter the family was moved to a large enclosure in the college greenhouse, where a shelf has been made into a sleeping box by the addition of a sliding door in which an aperture has been cut. For several minutes the family jumped and climbed and smelled about this new region. It was the mother who located the small aperture of the sleeping box and the dark quarters within. And after investigation it was she who began the conversational call which brought father and children to her side. The entire family is affectionate. The mother frequently caresses the young even though they are now more than a year old.

The maternal solicitude continued unabated and even when they were far too heavy to be carried, (up to 3 months), she still tried to lift them in her mouth and to get them back into the nest when the young were molested. After handling, also, she would lick them solicitously.

DEVELOPMENT OF THE YOUNG GALAGO.

From the beginning, as has already been stated, the young galagos could cling to surfaces and walk about on all fours. When not nursing, they were either under the mother, on her back (Pl. VI, Figs. 15, 16), or were curled up in a little nest made for them of soft tissue. In two weeks time there was a perceptible increase in size. Their pelt was heavier, but still homogeneous in color. They not only could walk about, but had begun to take small leaps of four and five inches, clumsily trying to balance on their hind legs, making efforts to climb on the struts of the cage and even to jump a few inches. Their bellies were very fat and their tails still curled somewhat. Between the second and third weeks, the young ones began to use the tongue in licking and grooming each other; they even began to lick me. When three weeks old they were approximately twice their original weights. They had minute incisor and canine teeth. They were very playful and would nip each other's tails and frolic about.

When four weeks old they could jump from the side of their cage a foot or more to its floor and back again. They could walk along a horizontal bar about a half-inch in diameter, sometimes losing their balance, but never their grip. They would now play with each other like kittens and could stand on their hind legs although their balance was still uncertain.

At six weeks the fur had become adult in appearance, the end of the hair assuming a lighter color, giving a frosted look. The chest and the lateral surfaces of the legs and arms were light orange-yellow. The longer, darker hairs standing out on the back, which are characteristic of the adult, were more conspicuous in the young ones, like a soft black fuzz. The dark markings on the face, however, were not yet as evident as those of the adult. At this time they began the moistening of the hand and foot-pads. They made great work of this operation, rubbing with energy the palm of the hand onto the sole of the foot on the same side. They scrubbed for some time, and were not completely sure of their balance.

The young galagos, which could jump from two to three feet in a horizontal position, watched with interest the action of their parents as they made vertical leaps from a window-sill and portiere to the picture molding. The first attempt at a vertical jump like those of the parents was made at the age of seven weeks when one succeeded in reaching the top of the window trim. One of the parents immediately jumped to a position beside it, and licked its fur. By the eighth week the young ones began coming down a perpendicular surface, gripping the edge in a regular adult fashion. At this time the young began making the protesting adult growl when handled. By the end of the second month, their balance was greatly improved and they could stand upright with considerable confidence.

From the age of one month the young attempted to eat solid food which was placed in the cage for the mother. By the end of the second month they were eating solid food regularly and drinking milk in considerable quantities.

Although still nursing, they were now so large that they had to be fed one at a time. By this time, the galagos had been moved into the country, and now occupied a screened-in porch, with freedom of action during the entire night. Flying moths were included in the diet of the parents. While at first the young had little interest in these flying insects, it grew as they watched the eagerness of the parents. They did not attempt to catch any themselves, but as the parents caught a moth, the young would try to take it away. The mother seems fairly willing to give up portions to her offspring. The samples were evidently pleasant, and by the twelfth week the young ones were capturing their own moths. They were not yet as quick or as dexterous as their parents, and even after succeeding in a catch, they frequently were obliged to give up their prize to a hungry parent. Picking up the discarded wings, the young would chew on the base of these for what nourishment there might remain. Cooke (1939) notes that adult Tarsius also chew on the base of moth wings. At three months of age they had learned to balance themselves on the rim of a jar and to dive in and extract the fluttering insect without loss of balance. By the end of the third month, the young had stopped nursing. The only evidence of infancy was the tendency to take moths from the mother, which she continued to permit them to do. They were now less rotund, and except for the soft black fuzz on their backs they looked like their parents in miniature.

SLEEP.

During sleep these animals have a tendency to crowd together, one frequently sleeping on top of another. In cold weather it is not unusual to find one adult completely hidden by a companion. They protect their eyes from the light by burying the head in the pelt of another galago. If the light is too intense, they try to crawl under any movable object for protection. At times, too, the tail is wrapped over the eye to exclude the light.

This variety does not usually sleep with the neck arched and the head tucked between the hind legs as does *Galago crassicaudatus*, although on rare occasions, when one *Galago s. moholi* has been isolated, I have seen this method employed. The large membranous ears remain somewhat folded during sleep.

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Appendix.

The activities outlined here occurred after the manuscript was in type. On the evening of December 7, 1940, oestrus recurred after an interval of six months. At this time a new factor was introduced. For some weeks prior to this date the young male, now twenty months old, had given evidence of sexual maturity with the result that, at the onset of oestrus, both males were accepted by the mother. The young female, however, has not yet become sexually active.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Head of adult male enlarged 2 ×. Crescent-shaped rhinarium shown with deep median cleft. Upper lip bounded by fur. No "snarling" expression of upper lip though animal is angry. Eyes with vertical pupils. Lashes visible on upper lid of eye to right. Vibrissae evident lateral, median to and below the eye, also at side of mouth on left. Note method of grasping small stick. Thumb and index finger on one side, the three outer fingers on the other.

PLATE II.

- Fig. 2. Life size group of family of four in characteristic sleeping position, taken when young were a year old. Note corrugation of ears of animals to right and lower center.
- Fig. 3. Photograph of family on rafter under porch roof. Upper eyelids of animal third on right shown extended over bulging eyes. This galago had been perched on the rim of the flash light reflector and was looking at the bulb when it was discharged. For a short time the animal was unable to tolerate even a subdued light.

PLATE III.

- Fig. 4. Photograph of hands $\times 2$. Illustrates method of resting palm on a flat surface with the flexed digits somewhat bent to one side. Note flat nails and pads along under surfaces of digits ending in enlargements at tips. Interdigital pads shown protruding beyond palm of hand to left.
- Fig. 5. Phalanges of hand flexed for grasping food. The two distal phalanges bend over the proximal phalanx of each digit except that of thumb. Thumb opposed.
- Fig. 6. Photograph of under surfaces of hand and foot, taken from the inside of a glass door on the outerside of which a galago is clinging. The index finger is shown to lie almost midway between the large space which separates the thumb and third finger. Illustrates the way in which the pads of the palm and sole flatten out when applied to a flat surface.
- Fig. 7. Photograph of under surfaces of feet taken when animal was in same position as in Fig. 6. The pads of the soles are not flattened out. Note fur-covered hinder portion of ventral surface of foot and large size of the pads of hallux, the interdigitals, thenar and hypothenar.

PLATE IV.

- Fig. 8. Photograph showing method of grasping branch by feet alone, leaving hands free for feeding.
- Fig. 9. The animal is hanging head down with hands free, grasping screen-trim by hind feet. Note the widely abducted, powerful hallux.

Fig. 10. Adult male and female. Male standing on toes reaching for insect. Note length of foot and hind limb. Tail serves as balancing structure. Digits of the hands are somewhat flexed, which is their usual position unless grasping food or perching.

PLATE V.

Figs. 11, 12, 13. Method of carrying young. (Fig. 11). Mother while on tabletop grasps young in region of shoulder. (Fig. 12). Young lifted from table, mother poised to jump to floor; feet of young drawn up. (Fig. 13). After jump, mother depositing young on floor.

PLATE VI.

Fig. 14. Photograph of young when two weeks old.

Figs. 15, 16, 17. Different postures when awakened from sleep. Young are about five weeks old. (Fig. 15). One baby under the mother, trying to get away from the light while the other lies on top of parent.

(Photographs reproduced as Figs. 1-10 were taken by Agnes Townsend; Figs. 11-17 enlargements of 16 mm. motion picture film taken by author).

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